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DISTAL SETAL MECHANORECEPTORS OF THE FIRST ANTENNAE OF MARINE COPEPODS

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ABSTRACT

The first antennae (antennules) of many calanoid copepods can be divided into three sectors differing in setal arrangement, type, and number: the proximal sector where setae can be closely spaced; a middle sector where setae tend to be sparse; and the distal tip where several setae form a tuft. Each sector of the first antenna also lies within different flow regimes of the field created by the copepod during normal swimming and feeding activities (Fields and Yen, 1993): the distal tip experiences flow velocities that are much slower than the proximal sector. Extracellular recordings of mechanosensory discharges from the antenna during controlled mechanical stimuli (Gassie et al., 1993) show large-spike (>300 μV) neural responses from a small number (<10) of units, as well as activity from numerous smaller units. When the distal tip is removed, the large spiking units, but not all of the smaller ones, disappear. The large action potentials may be transmitted by the large-diameter (>5 μm) axons present in the distal region of the antenna. The large spiking units are sensitive to near-field displacements and respond to high frequency stimuli. Threshold sensitivities can reach less than 10 nm at 1,000 Hz. The spike amplitudes and sensitivity of these distal receptors suggest that they may be used to trigger responses that require short reaction times such as in rapid escapes. Since prey entrained in the flow are captured closest to the proximal sector of first antennae, a possible role for setal receptors here would be to detect prey signals (movements, chemical exudates), while out in the quiet region near the distal tip, the setal receptors may be sensing water displacements generated by more distant objects (e.g., obstacles or predators).

Aquatic animals from many taxa (e.g., fishes, molluscs, crustaceans, annelids, chaetognaths) depend on mechanosensors to obtain critical information about their environment. Behavioral evidence suggests that mechanoreception is important in copepod predator-prey interactions (Haury et al., 1980; Buskey, 1984; Gill, 1986; Gill and Poulet, 1988; Tiselius and Jonsson, 1990). The presence of mechanosensors in copepod first antennae (or antennules) is supported by morphological analyses (Strickler and Bal, 1973; Friedman, 1980; Yen et al., 1992). Knowledge of the physiological properties of the receptors should contribute to the understanding of the role of mechanoreception in copepod behavior and ecology.

We have made physiological recordings from copepod antennae that suggest that they have mechanosensory properties very different from the better studied fish, squid and decapod mechanosensory systems (Wiese, 1976; Budelmann and Bleckmann, 1988; Coombs and Janssen, 1990; Wiese and Marschall, 1990; Yen et al., 1992). This led us to hypothesize that the fluid environment of the copepods and the relevant mechanical stimuli are distinct from those of other animal groups. Therefore, in addition to the physiological studies, more information is necessary about the specific location of the antennal mechanosensors and how this correlates with the fluid environment around the antenna. This information is basic to the understanding of copepod food-search and predator-avoidance behaviors. Because of their location, it has been hypothesized that the setae on the distal antennal segment may play an important role in gathering sensory information (Haury et al., 1980; Gill, 1986). In the present study, we characterized the hydrodynamic environment and mechanoreceptive properties of distal antenna regions in two calanoid copepod species, *Euchaeta rimana* and *Pleuromamma xiphias.* These two species belong to two common copepod genera and their distribution patterns

(McGowan and Walker, 1979; Ambler and Miller, 1987), food preferences (Finn, 1983; Yen, 1988; Bennett and Hopkins, 1989), and behavior (Morris et al., 1985; Yen et al., 1991) have been investigated.

Materials and Methods

Collections.—*Euchaeta rimana* were collected 1.5 km outside of Kaneohe Bay, Oahu, Hawaii by subsurface tows with a 333-μm mesh net (50 cm diameter, 2 m long). *E. rimana* were sorted into 2-liter jars and maintained at ambient light and temperature (20° to 24°C). *Pleuromamma xiphias* were collected from a deep pipe (intake depth 586 m) at the Natural Energy Laboratory of Hawaii at Keahole Point, Island of Hawaii. A 183-μm mesh net was attached to a 30.5 cm diameter, 800-m-long PVC pipe and animals were removed and sorted every 6 to 8 h. Intact *P. xiphias* were placed into 2-liter jars and maintained at 6° to 8°C. Both *E. rimana* and *P. xiphias* were fed freshly-hatched *Artemia* nauplii. Only actively swimming animals with intact antennae were used in the research.

Antennal Drawings.—The antennal drawings were made from photomontages of the first antennae photographed through a compound microscope (Leitz Ortholux) at 25× or 40×. Live animals were stained with Azure II, immobilized by cooling, placed under a cover slip, and examined by microscope. If the antenna was intact, it was photographed (Wild Photoautomat MPS 55 System).

Transmission Electron Microscopy.—To improve fixation of the antenna, the animals were cut with iridectomy scissors behind the head prior to fixation. Animals were preserved in 4% glutaraldehyde in 0.1 M sodium cacodylate buffer with 0.35 M sucrose, decalcified for 1 to 1.5 h in fixative with 2% disodium EDTA, then returned to buffered glutaraldehyde for 0.5 h, before being washed in buffer. Animals were post-fixed in 1% osmium tetroxide and dehydrated in a graded ethanol series and propylene oxide, then embedded in LX112. Thin sections through the antenna, made on a Reichert Jung Ultracut E microtome, were double stained with uranyl acetate and lead citrate, and viewed and photographed in a Zeiss 10/A TEM at 80 kV.

Flow Fields.—The movement of 20-μm polystyrene spheres (Polysciences) entrained in the flow field generated by the second antennae of tethered *Euchaeta rimana* and *Pleuromamma xiphias* was visualized by fixed-frame laser-illuminated video-imaging techniques (duplicating Strickler, 1985). Analyses of particle pathlines, tracking the water flow within a narrow corridor above and along the first antennae, permitted calculations of the velocity gradient surrounding the first antennae. Further methodological details are described in Fields and Yen (1993).

Physiological Recordings and Mechanical Stimulation.—For the physiological recordings, an individual copepod was held in forceps and drawn into mineral oil, with one antenna projecting downward into the seawater. Extracellular nerve impulse traffic was recorded between the forceps and seawater. The signal was amplified 1,000× (*P. xiphias*) or 10,000× (*E. rimana*), displayed on a dual-beam oscilloscope, digitized and stored on microcomputer. For the ablation experiments, the last antennal segments (segment 23–25 for *P. xiphias* and segment 21–22 for *E. rimana*) were removed with iridectomy scissors.

For the analysis, ASCII files were generated from the stored binary data files. From the stimulus files, maximum displacements and frequencies were calculated using in-house BASIC programs. Water displacements were generated by a sphere (3 mm diameter) moved by an electromagnetic pusher (Ling 203). Displacements at the antenna were calculated using dipole equations (Harris and van Bergeijk, 1962; Kalmijn, 1988). The physiological records were examined for the presence and timing of spiking events. Other methodological details are discussed in Gassie et al. (1993).

Results

External Morphology.—A copepod's first antenna has 28 original segments (Huys and Boxshall, 1991). The actual number of segments varies between sexes and among species due to fusion. The adult *Pleuromamma xiphias* female has 25 segments, whereas the adult *Euchaeta rimana* female has 22 segments (Fig. 1). The first antenna can be divided into three sections: closest to the head the segments tend to be narrow and densely populated by short setae, with one or more long setae projecting anteriorly. In the genus *Euchaeta,* these setae are very long and they have an unusual 90° bend (see Yen and Nicoll, 1990 for details). In the middle section (segments 12 to 21 for *P. xiphias,* segments 13 to 19 in *E. rimana*) the segments elongate and setae occur at a lower density. The distal segments are

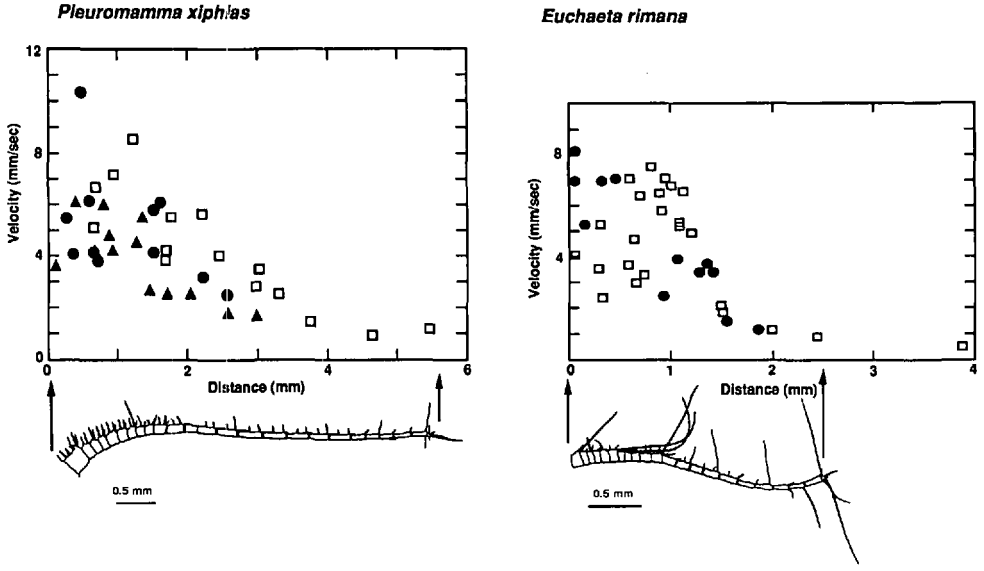


Figure 1. Flow velocities along and drawings of the first antennae (dorsal view, anterior up) of *Pleuromamma xiphias* (A) and *Euchaeta rimana* (B) females. Different symbols represent velocity measurements from different individuals.

characterized by the presence of two very long setae (>500 μm), one pointing anteriorly, and the other posteriorly.

Flow Fields.—The proximal section of the antennae experiences the highest flow velocities generated by the copepod (Fig. 1). The smallest flow velocities (ca. 1 $mm \cdot s^{-1}$) were measured near the distal tip and there was a factor of 5 to 10 difference in the maximum versus minimum velocities. Analyses of the flow fields of *P. xiphias* and *E. rimana* show that the distal tips protrude out of the high velocity region. The high velocities in the proximal region are induced by the copepod with the paddling of its second antennae (Fields and Yen, 1993; Yen et al., 1991).

Near-field Receptors.—Recordings of the nerve impulse traffic from the central and distal sections show increased neural activity during mechanical stimulation (Figs. 2A, C, 3A, C). *P. xiphias* has giant spiking units (300 to 3,000 μV), whereas the largest units recorded in *E. rimana* were less than 150 μV. These two neural patterns, the presence of a few large spikes (>300 μV) vs. only small spikes (<150 μV), represent the two general patterns of copepod neural responses to mechanical stimuli observed by Yen et al. (1992).

The antennal mechanosensors are responding to near-field displacements, as is shown in the log-log plot of threshold sensitivities versus distance from the dipole (Fig. 4). Near-field displacements drop off with the cube of distance (Bergeijk, 1967; Kalmijn, 1988), and the slopes of the log-log plots are not significantly different from 3 (Table 1). The slopes are significantly different from 2 (Table 1), which is the predicted relationship between threshold and dipole distance if the receptors were responding to far-field vibrations. However, one would not expect the copepods to be sensitive to far-field vibrations (or sound), since they are virtually the same density as seawater (Hawkins and Myrberg, 1983).

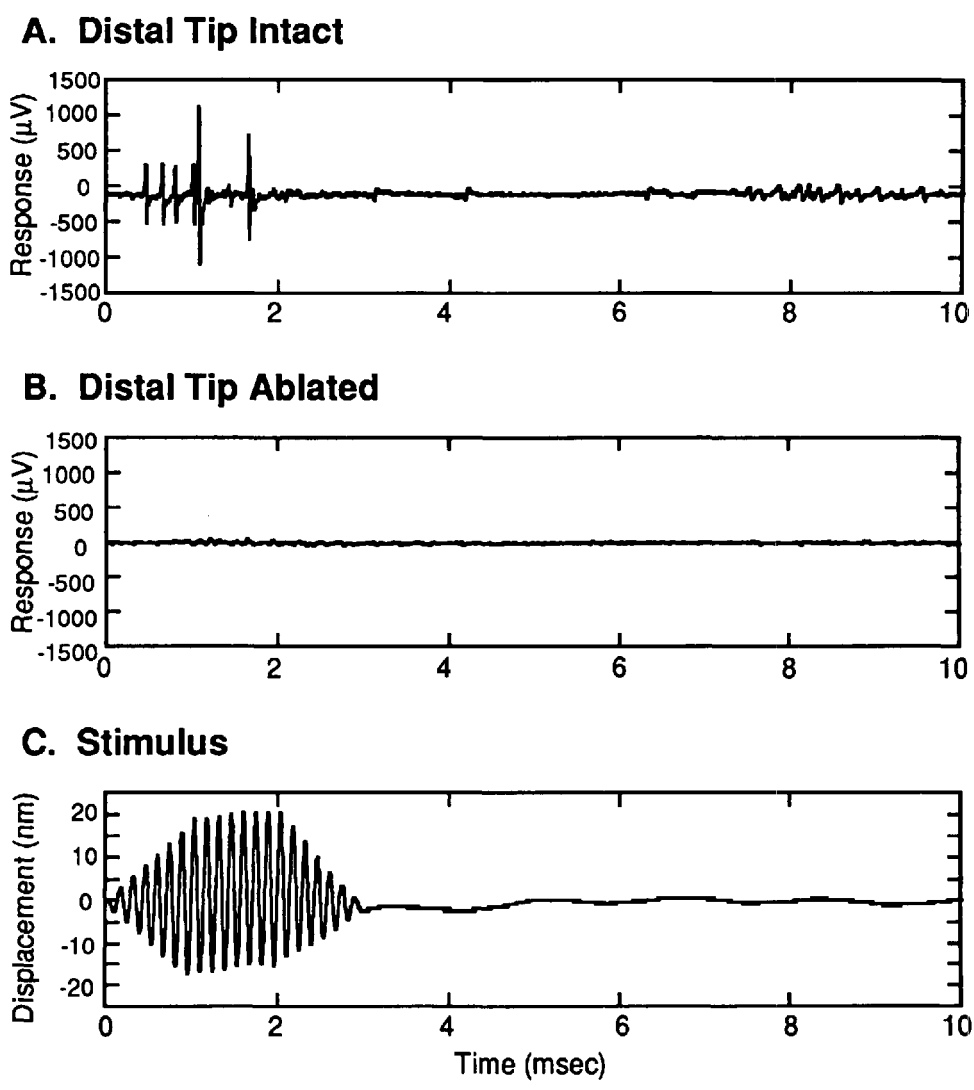


Figure 2. A. Extracellular recordings from the first antenna of *Pleuromamma xiphias* with the distal tip intact. B. Extracellular recording with the distal tip ablated at the second-to-last segment. C. Mechanical stimulus as recorded by the displacement sensor, scaled to the near-field displacement at the antenna (frequency = 700 Hz, threshold diplacement = 7 nm).

Sensitivity to Water Vibration.—Threshold sensitivities were measured using sinusoidal stimuli with a trapezoidal envelope. In both species, sensitivity increased with stimulus frequency from 30 Hz to 1,100 Hz (Fig. 5). Threshold sensitivities to diplacements of less than 10 nm were found in *Euchaeta rimana* and near 10 nm in *Pleuromamma xiphias* at frequencies of 800 to 1,100 Hz. The largest difference in sensitivity between the two species occurred at 100 Hz: threshold for *E. rimana* was ca. 10 nm, whereas *P. xiphias* had a threshold near 50 nm. Threshold sensitivities to 10 nm displacements were previously found in *Labidocera madurae* using a single cycle stimulus (Yen et al., 1992).

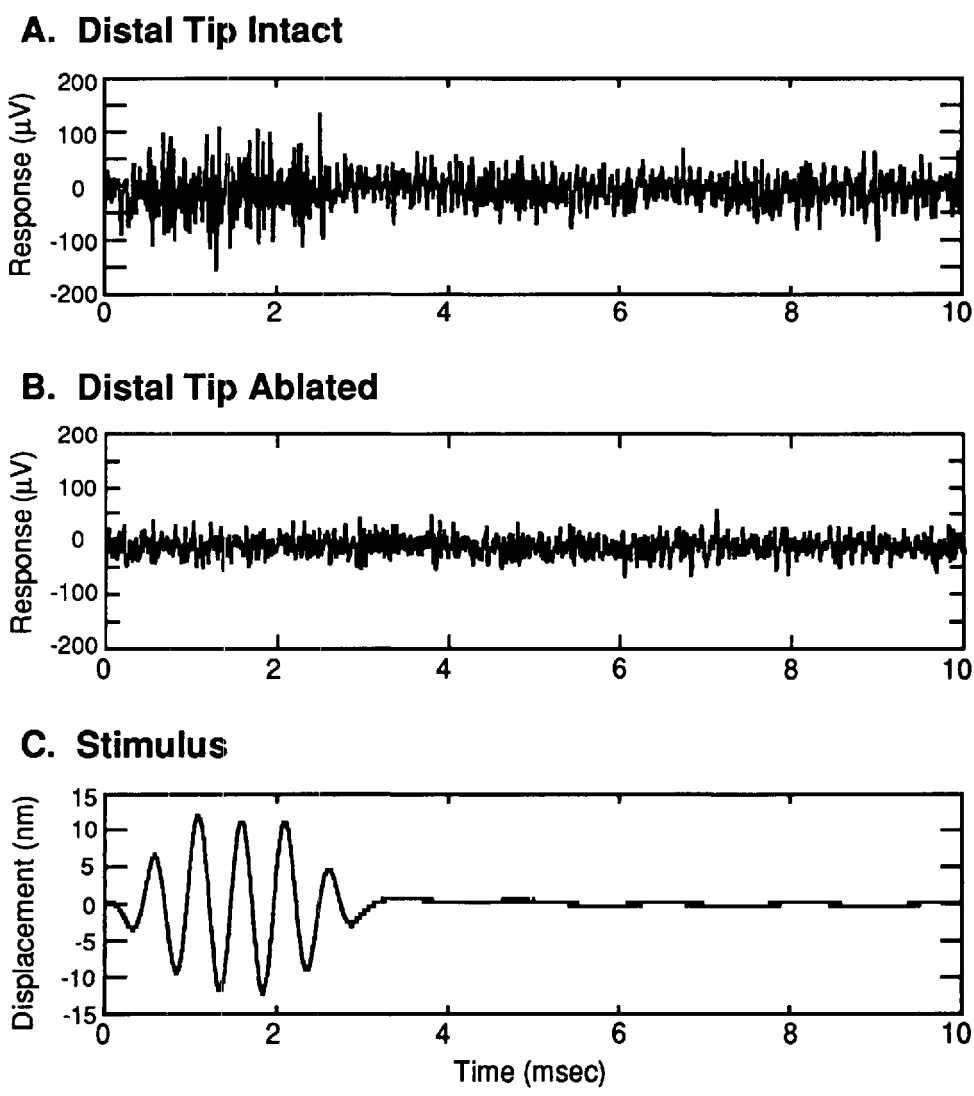
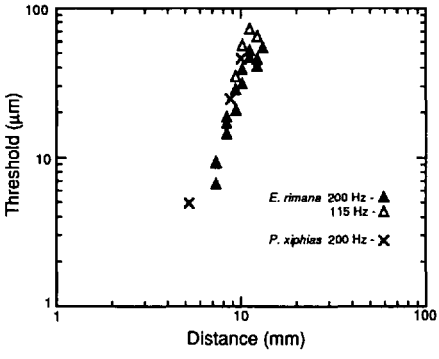


Figure 3. A. Extracellular recordings from the first antenna of *Euchaeta rimana* with the distal tip intact. B. Extracellular recording with the distal tip ablated at the second-to-last segment. C. Mechanical stimulus as recorded by the displacement sensor, and scaled to the near-field displacement at the antenna (frequency = 200 Hz, threshold displacement = 9 nm).

Location of Mechanosensors.—Ablation of the distal two segments caused the disappearance of the larger units in *P. xiphias* and *E. rimana* (Figs. 2B, 3B). This indicated that the high-frequency-sensitive units are in the distal setae. These units could not be re-activated at even larger stimulus amplitudes. However, in *P. xiphias,* it was possible to activate smaller (<50 μV) units at larger displacements. Presumably this activity came from mechanosensory hairs located more proximally on the antenna shaft.

Internal Morphology.—TEM cross-sections through the antenna through segment 17 of *Pleuromamma xiphias* indicated the presence of at least three large neural



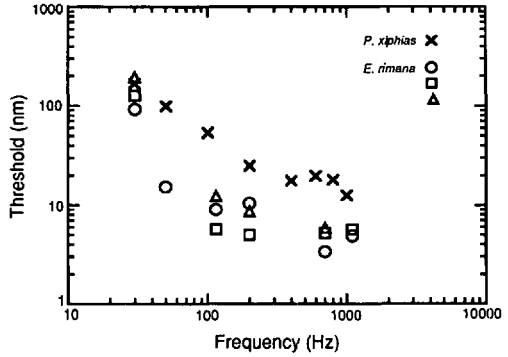


Figure 4 (left). Threshold as a function of dipole distance measured in *Pleuromamma xiphias* at 200 Hz (crosses) and *Euchaeta rimana* at 200 Hz (filled triangles) and 115 Hz (open triangles). The slopes are not significantly different from 3, indicating response to near-field displacements.

Figure 5 (right). Threshold sensitivities for *Pleuromamma xiphias* (crosses) and *Euchaeta rimana* (open symbols) females between 30 and 1,100 Hz.

processes (diameter: 5–6 μm, Fig. 6). Because amplitude of extracellularly recorded impulses is positively correlated with axon diameter in a variety of organisms, this further suggests that the large units sensitive to mechanical stimuli originate in the setae on the distal segments. The micrograph also shows the insertion of a mechanosensory seta, as indicated by the presence of microtubule bundles (Fig. 6).

Discussion

To summarize, a steep velocity gradient is found in the water surrounding the antennae where the distal tip protrudes out of the flow field into a region of low flow velocities in tethered animals. Neural responses from the distal tips are transmitted by the larger spiking units in both *P. xiphias* and *E. rimana.* The large impulses in *P. xiphias* are likely to be transmitted by the large diameter neural processes originating in the distal sector of the antennae. This suggests that the distal tips are used to sense disturbances that require fast reaction times, such as those involved in escape responses.

The most distinct feature of the copepod antennal mechanosensors is the high sensitivity (10 nm) at high frequencies. This result is surprising for two reasons: 1) fish lateral line and most decapod mechanosensors have peak sensitivities below 400 Hz (Laverack, 1968; Taylor, 1968; Tazaki and Ohnishi, 1974; Wiese, 1976; Tazaki, 1977; Barth, 1980; Tautz et al., 1981; Fay, 1988; Coombs and Janssen, 1990); and 2) mechanical stimuli possibly relevant to the animal, such as the beating of copepod appendages have been measured at frequencies below 100 Hz

Table 1. Threshold sensitivity as a function of stimulus distance

	Frequency	N	Slope	SE	Y-intercept	r^2
Pleuromamma xiphias	200 Hz	3	3.36	0.26	2.16	0.997
Euchaeta rimana	200 Hz	13	3.34	0.34	1.74	0.947
	115 Hz	5	3.46	0.66	1.93	0.935

Slopes are not significantly different from 3 (near-field displacement, Kalmijn, 1988), using the *t*-test (one-tailed test, $P > 0.2$, Sokal and Rohlf, 1969). Slopes are significantly different from 2 (far-field displacement, Kalmijn, 1988; one-tailed test; *E. rimana*: 200 Hz, $P < 0.001$; 115 Hz, $0.01 < P < 0.05$; *P. xiphias*: 200 Hz, $0.05 < P < 0.1$).

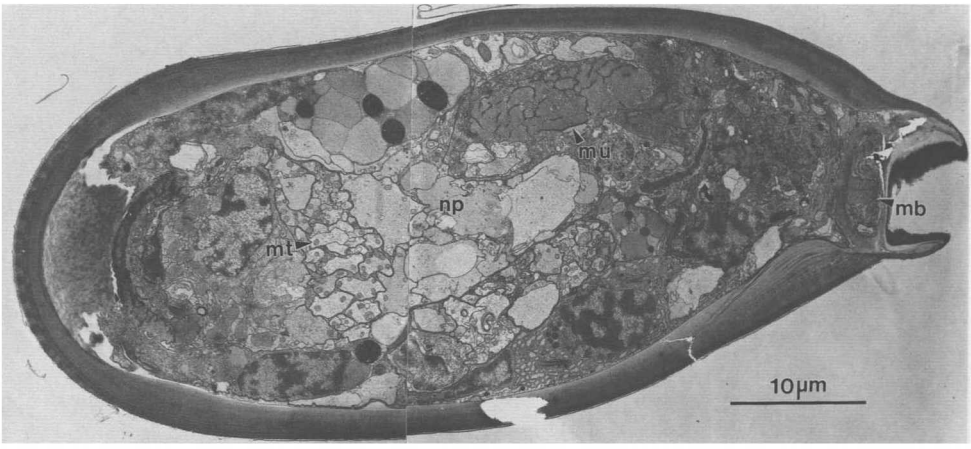


Figure 6. Transmission electron micrograph through the 17th segment of *Pleuromamma xiphias*. Arrows point to neural processes (np), muscle (mu), mitochondria (mt), microtubular bundle (mb).

(Kirk, 1985; Strickler, 1985; Price and Paffenhöfer, 1986; Gill and Poulet, 1988). The large-spike copepod antennal receptors we have examined so far are relatively insensitive at frequencies below 200 Hz. High frequency vibrations (1 kHz) were reported to be produced by two *Diaptomus* species (Giguère and Dill, 1979). The source of these high frequency acoustic signals is unclear, and because of differences in methodology, it is difficult to compare the amplitudes of these high frequency signals with those of the signals produced by the beating of the appendages.

Giguère and Dill (1979) were interested in the 1 kHz acoustic signal because they had found this frequency to be optimal for eliciting striking responses in a

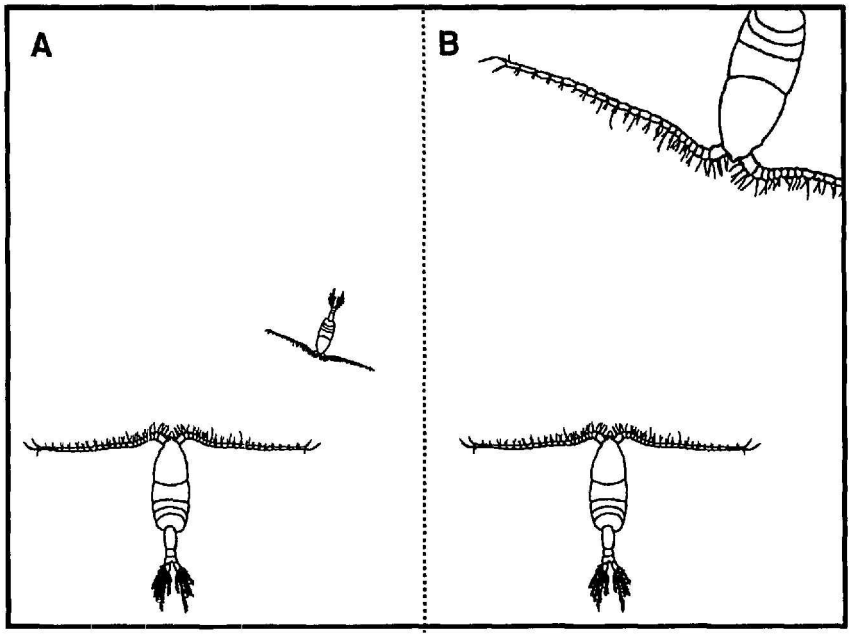


Figure 7. Hypothetical situation where a copepod is approached by A) a prey, and B) a predator.

Table 2. Hypothetical predator-prey interaction: detection distance

	Radius (mm) A	Distance (mm) R	Water displacement (nm) U	θ	Threshold (nm) D
Prey	0.1	0.46	1,000	0°	10
(0.5 mm)	0.1	0.37	1,000	90°	10
Predator	1.5	6.96	1,000	0°	10
(7 mm)	1.5	5.53	1,000	90°	10

Dipole Equation: $D = (A^3/R^3) \cdot U \cdot (\cos\theta + 0.5 \sin\theta)$, $\theta = 0°$; 90°, from Kalmijn (1988). Equation was solved for R.
Illustrative only: For detector stationary and optimally oriented, conditions not always met naturally.

pelagic freshwater predator, *Chaoborus trivitattus* larvae. Sensitivities extending to higher frequency (>300 Hz) stimuli have been reported for *Euphausia superba,* a pelagic crustacean (Wiese and Marschall, 1990). Mechanosensors on the antennular flagella appear to be velocity detectors. Wiese and Marschall were unable to obtain a best frequency, since sensitivity in *E. superba* increased throughout the frequency range tested (0.5–400 Hz). However, threshold displacements in *E. superba,* 200 nm at 400 Hz, are comparable to thresholds in decapod mechanosensors, and one order of magnitude larger than in the copepods (Yen et al., 1992; present study). These studies suggest that in the pelagic environment there may be a need for sensing high frequencies, and the copepods, in particular, have evolved highly sensitive mechanosensors. In view of these results, it may be appropriate to focus attention on these sensory capabilities when designing behavioral studies, since only then might we understand the relationship between sensory physiology and ecology.

Haury et al. (1980) suggested that since the distal tip of the first antennae extend far from the copepod's body, they may be sensing different signals than those detected by receptors on the body. The distal tips are characterized by the presence of multiple, long setae. The first antennae can be as long as or longer than one body length in some calanoid copepods (e.g., *Pleuromamma xiphias, Centropages longicornis*; Yamaji, 1976). The setae on the distal tip are fairly distant from the animal itself, and somewhat isolated from the flow fields generated by the appendages (Fig. 1). Thus, the setae may be optimally located in sense vibrations originating from predators or prey. The ablation experiment, identifying the distal hairs as the source of the giant spikes, reinforces the view that these hairs play an important role as an early warning system, monitoring critical mechanical information in the environment.

In Figure 7, we present a hypothetical situation, where a 3-mm copepod (cephalothorax length) is approached by A) a potential prey, a 0.5-mm copepod; and B) a potential predator, a 7-mm copepod. Assume, for the sake of argument, that a copepod generates water disturbances equivalent to those of a sphere of similar dimensions (estimated radii: 0.1 mm for prey and 1.5 mm for predator). The near-field displacements produced by them will decline as the cube of the distance, so one can then calculate detection distances using the dipole equations (Table 2). If the copepods (0.5 mm and 7 mm) are generating 1 μm water displacements, then the prey animal (0.5 mm) could be detected at ca. 0.3 mm distance, whereas the predator (7 mm) would be detectable 5.5 to 7 mm away. Furthermore, because the prey copepod is small compared to the length of the first antenna, the 3 mm copepod would be detecting its presence primarily with the mechanosensors on one distal tip. In contrast, the large predator (7 mm) would be detected simultaneously by the sensors on both distal tips, which could permit spatial localization (Fig. 7). In general, zooplankton appear to be subject to high predation rates

throughout their planktonic existence. Predator detection, and hence the antennal mechanosensors may be critical for the survival of individual copepods.

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